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Biological characteristics of silver-phase Japanese eels, *Anguilla japonica*, collected from Hamana Lake, Japan

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Abstract—The biological characteristics of 259 silver-phase Japanese eels, *Anguilla japonica*, were investigated in Hamana Lake, Japan from 2003 to 2007, to obtain basic data for this species at the downstream migration. Their silvering stage, condition factor, three internal (gonad-somatic index: GSI, hepato-somatic index and gut index) and two morphometric (fin index and eye index) indices were calculated. The overall sex ratio tended to be female (61%), but the sex ratio differed among years and months. Silver eels of S1 stage (early silver) were predominant than S2 (late silver) for both sexes (female: 67%, male: 77%). Female eels attained to larger size (mean: 659.3 mm) and older age (9.9 years) than males (527.7 mm and 8.3 years). The GSI increased from October to December whereas gut index decreased with months, but significant change in morphometric indices were not found within silver-phase. The results of this study suggest that silver-phase Japanese eels have a wide range of the biological characteristics, but significant differences can occur in sex ratio and the proportion of silvering stages among years, and in internal indices within silver-phase during their downstream migration season.

Key words: *Anguilla japonica*, silver eels, sex ratio, silvering index, GSI, morphometric index, age, growth.

Introduction

Japanese eel, *Anguilla japonica*, is widely distributed in East Asia from Taiwan, through eastern China, and north to Korea and Japan (Tesch 1977), and is an important commercial fisheries and aquaculture species with a catadromous life history (Matsui 1972, Tsukamoto et al. in press). This species spawns far offshore in the ocean to the west of the Mariana Islands in the western North Pacific (Tsukamoto 1992, 2006), but its growth phase occurs in freshwater or in estuarine and coastal areas as yellow eels (Tsukamoto et al. 1998, Tsukamoto and Arai 2001, Yokouchi et al. 2008). After 5–15 years of the yellow eel growth phase, Japanese eels metamorphose into the silver eel stage, with maturing gonads and enlarging eyes (Aoyama and Miller 2003, Han et al. 2003a), and they move back downstream to the ocean and begin their migration to the spawning area. These changes are thought to be an adaptation to the marine environment for spawning migration (Pankhurst 1982). Recently, serious declines of the Japanese eel stock have been documented (Tatsukawa 2003), thus, there is an urgent need for effective resource management based on accurate ecological information.

Previous ecological studies on Japanese eels were mostly focused on their early life history such as the migration of their oceanic larvae, called leptocephali, and the recruitment mechanisms of juvenile glass eels (e.g., Tsukamoto 1990, Ozawa et al. 1991, Tsukamoto et al. 1992, Arai et al. 1997, Kimura and Tsukamoto 2006). Consequently, knowledge about their early life history has accumulated during last few decades. After their recruitment into the rivers and estuaries, studies about migratory histories of eels were only intensively investigated (Tsukamoto and Arai 2001, Tzeng et al. 2002, Shiao et al. 2003, Kotake et al. 2003, Daverat et al. 2006). There is a general lack of knowledge about the basic biological information such as sex ratio, age and growth and the maturation at the downstream migration of the silver eels of this species compared to other anguillid species (Tsukamoto et al. in press).

Some recent studies have been done on the silvering stages (Okamura et al. 2007), the environmental triggers of the spawning migration (Okamura et al. 2002), ovarian morphology (Utoh et al. 2004) of silver-phase Japanese eels in Japan. There also have been studies on the occurrence of silver eels in the East China Sea (Sasai et al. 2001), or on the growth rates (Tzeng et al. 2000, 2003), gonadal morphology (Han et al. 2003a) and reproductive physiology (Han et al. 2003b). Although basic ecological studies of the Japanese eel are important to understanding the ecology of this species during its silver phase, these are still lacking in most parts of its range.

The objective of the present study was to investigate the biological characteristics of silver-phase Japanese eels during the downstream migration season in the Hamana Lake system, Japan. Their demographic attributes (size, morphology, condition, age, growth and degree of maturation) were obtained to provide important basic ecological information about the Japanese eel. This is the first study to use a large number of male silver eels for investigation of their biological characteristics compared to the other coastal areas.

Materials and methods

Collections of eels

We collected a total of 259 silver-phase Japanese eels in Hamana Lake (Fig. 1), Japan from 2003 to 2007. The Hamana Lake system is located in central Japan (34°45 N, 137°35 E), and is comprised of Hamana Lake, adjacent lakes with more than 17 inlet rivers or streams. In this study, silver eels were collected by the set nets (mesh sizes of 18 or 22 mm and lead/wing lengths of 180 m) in center or lower part of Hamana Lake (Fig. 1). Hamana Lake is a brackish lake with salinity ranging from 22 to 33 psu depending on the tide, with a connection to the Pacific Ocean only by the Imakireguchi channel (200 m width). The water surface area of Hamana Lake is 65 km^2 and its mean depth is approximately 4.8 m. Silver eels were collected during downstream migration seasons. From 2005 to 2007, about 30 silver eels were collected within each month to cover the high season (usually October or November) of their downstream migration (2 months in each year). From 2003 to 2004, silver eels were collected as annual additional samples, because we did not collected large number of silver eels during the season.

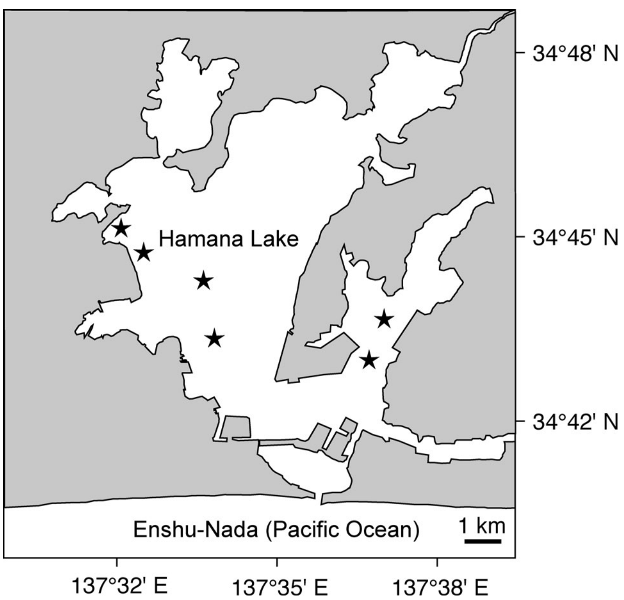

Fig. 1. Map of sampling sites in the Hamana Lake system, Japan. Set net sites are depicted by stars.

Stage of maturation

The total length (TL) of all eels was measured to the nearest 1 mm, and body weight (BW) to the nearest 0.1 g. Left pectral fin length (L_p), horizontal and vertical orbital diameters (left eye) were measured to the nearest 0.1 mm. Gonad (GW), liver (LW) and digestive tract (DW) (including stomach and intestine) weights were measured to the nearest 0.1 g and sex was determined by visual inspection of gonad morphology. The silver-phase was confirmed by examination of color of fish body, and after 2005 sampling, silvering stage (S1; early silver or S2; late silver) was recorded by examination of body color and pectoral fins following Okamura et al. (2007).

Based on these variables, Fulton's condition factor (K), internal and morphometric indices: gonad-somatic index (GSI), hepato-somatic index (HSI), gut index, fin index, eye index (Pankhurst 1982) were calculated as follows:

$$K = BW\,(g)/TL^3\,(cm) \times 100$$

$$GSI = GW\,(g)/BW\,(g) \times 100$$

$$HSI = LW\,(g)/BW\,(g) \times 100$$

$$\text{Gut index} = DW\,(g)/BW\,(g) \times 100$$

$$\text{Fin index} = L_p\,(mm)/TL\,(mm) \times 100$$

$$\text{Eye index} = [(A+B)/4]^2 \times \pi/TL\,(mm) \times 100$$

where A is the horizontal orbital diameter (mm), B is the vertical orbital diameter (mm).

Age and growth

A total of 149 silver-phase Japanese eels collected in Hamana Lake from 2003 to 2007 were used for age determinations using their otoliths. The extracted otoliths were embedded in epoxy resin (Struers, Epofix) and ground to expose the core along the anterior-posterior direction in the frontal plane using a grinding machine equipped with a diamond cup-wheel (Struers, Discoplan-TS). They were polished further with OP-S liquid (Struers). The otoliths were etched with 1 % HCl, and thereafter stained with 1% toluidine blue. The age of specimens was determined by counting the number of blue-stained rings or annuli separated by transparent zones outside the elver mark. In this study, we assumed that the otolith rings were deposited annually, and assigned the distinct check (elver mark) (Arai et al. 2003) thought to be associated with inshore entrance of growth habitat as age=0. Annual growth rate (mm/year) was estimated by size and age (Tzeng et al. 2000) as follows:

$$\text{Growth rate} = [TL\,(mm) - 60]/\text{Age (year)}$$

where 60 is the mean total length of glass eels when they entered to continental growth habitats (Tsukamoto 1990, Tzeng et al. 2000).

Growth curves of silver-phase Japanese eels were described using the von Bertalanffy growth equation for each sex as follows:

$$L_t = L_\infty[1 - e^{-k(t-t_0)}]$$

where L_t is the length at age t, L_∞: the maximum theoretical length towards which the length of the eel tends, k: the growth coefficient (the rate at which the length approaches L_∞), and t_0: the (hypothetical) time at which the eel would have been zero size if it had always grown according to the von Bertalanffy equation.

Data analysis

General linear model was used to determine whether there were significant variations among years or months in the size (TL, mm), condition (K), internal (GSI, HSI, gut index) and morphometric (fin and eye index) indices of silver eels. The data were analysed by multivariable linear model:

$$\text{Dependent variable} = \gamma_0 + \gamma_1\text{Sex} + \gamma_2\text{Year} + \gamma_3\text{Month} + \gamma_4\text{Year}\times\text{Month}$$

where γ_i are the coefficients of variables in models, Year× Month indicate the interaction between these variables.

Differences in the sex ratios or the proportion of silvering stages among years and months were assessed using a χ^2 test. The Mann-Whitney U-test was used to compare the size, indices, age and growth between sexes or stages. Statistical analyses were performed with program Statistica ver. 7 (StatSoft, Inc.) for linear modeling, and Prism ver. 4.0c (GraphPad Software, Inc.) for the other general statistics. Microsoft Excel 2004 (Microsoft Corp.) for calculating parameters of the von Bertalanffy growth curve.

Results

Sex ratio and silvering stage

The silver-phase Japanese eels (*Anguilla japonica*) collected from Hamana Lake were predominantly females in total catch (61%, n=159), but certain amount of males were found (n=100, Fig. 2). There was a significant variation in the sex ratio among years (χ^2 test, $p<0.001$, Fig. 2). Silver eels collected from Hamana Lake were predominantly S1 for both sexes (67%, n=97 for females, 77%, n=68 for males, Table 1). There was a significant variation in the proportion of silvering stages among years (χ^2 test, $p<0.001$). Whereas, the proportion of silvering stages were similar between sexes in 2006 and 2007 (χ^2 test, p=0.34–0.97, Fig. 3) and statistical test was not performed for 2005 because of small sample size of S2 (n=1). The development of silvering was observed from November 2006 (75% S1, n=12 for females, 67% S1, n=6 for males) to December 2006 (28% S1, n=8 for females, 31% S1, n=5 for males, Fig. 3).

Table 1. Biological characteristics of silver-phase Japanese eels collected in Hamana Lake from 2003–2007.

Sex	Stage	n	Total length (mm)	Body weight (g)	Condition factor	GSI	HSI	Fin index	Eye index	Gut index
Female	S1	97	656.8±60.7	471.3±155.2	0.16±0.02	2.15±0.49	1.40±0.29	5.40±0.46	3.30±0.59	0.69±0.34
			509–804	181–859	0.12–0.20	0.92–3.62	0.89–2.26	4.60–7.09	1.82–4.98	0.31–2.00
	S2	47	669.1±65.1	487.4±160.4	0.16±0.02	2.72±0.52	1.50±0.30	5.50±0.35	3.67±0.65	0.59±0.19
			512–794	196–782	0.12–0.20	1.49–4.03	1.08–2.50	4.66–6.20	2.45–5.13	0.29–1.01
	Total*	159	659.3±65.6	474.2±164.3	0.16±0.02	2.28±0.59	1.43±0.29	5.38±0.45	3.37±0.64	0.66±0.30
		144**	476–804	160–1034	0.12–0.20	0.47–4.03	0.89–2.50	4.22–7.09	1.82–5.13	0.29–2.00
Male	S1	68	524.2±46.1	218.2±60.5	0.15±0.02	0.32±0.13	1.54±0.36	5.36±0.51	3.15±0.56	0.78±0.27
			426–615	107–350	0.09–0.27	0.15–0.74	1.02–2.66	3.99–6.44	2.26–5.08	0.26–1.43
	S2	20	544.8±48.9	236.9±65.8	0.14±0.01	0.42±0.09	1.64±0.34	5.74±0.41	3.34±0.51	0.60±0.12
			430–633	109–383	0.11–0.17	0.29–0.59	1.09–2.29	4.92–6.30	2.59–4.31	0.45–0.84
	Total*	100	527.7±47.7	219.8±61.4	0.15±0.02	0.33±0.13	1.56±0.36	5.39±0.54	3.10±0.60	0.74±0.25
		88**	413–633	106–382	0.09–0.27	0.10–0.74	1.02–2.66	3.96–6.44	1.60–5.08	0.26–1.43

Note: upper numbers: mean±SD; lower: range, * total include silvering stages were not determined, ** indicate number of samples of HSI and gut index.

Size and condition

The body sizes of the female silver eels examined in this study were considerably larger than those of the males (Table 1, Fig. 4). The TL of the females (n=159) ranged from 476 to 804 mm, with a mean±SD of 659±65.4 mm. The TL of the males (n=100) ranged from 413 to 633 mm, with a mean of 527±47.7 mm. The BW of females (n=159) ranged from 160 to 1034 g, with a mean of 474±164 g, and that of males (n=100) ranged from 106 to 383 g, with a mean of 220±61.4 g (Table 1). BW of eels was exponentially increased with TL for females and males ($BW=0.3\ TL^{3.4}\times 10^{-3}$, $r^2=0.90$ and $BW=0.2\ TL^{2.9}\times 10^{-2}$, $r^2=0.85$, respectively). The condition factor (K) of female eels ranged from 0.12 to 0.20 with a mean of 0.16±0.02, and those of males ranged from 0.09 to 0.27 with a mean of 0.15±0.02. The females collected in this study were significantly larger in both TL and BW than those of the males (Mann-Whitney *U*-tests, $p<0.001$). Statistical difference in size of female silver eels between stage S1 and S2 was not found (S1: 657 mm, n=97, S2: 669 mm, n=47, Mann-Whitney *U*-test, p=0.21, Fig. 4). Size of male silver eels of stage S1 (524 mm, n=68) was not significantly different from those of stage S2 (544 mm, n=20) (Mann-Whitney *U*-test, p=0.07, Table 1).

The body sizes of female eels did not differ among years and months revealed by linear modeling (Table 2). In these models, Year, Month and the interactions between these variables were not significant to the size and condition of the silver eels (Year, Month, Year×Month, $p>0.05$, Table 2, Fig. 5, 6). This indicated that there was no significant variation in eel size and condition among years and months (Table 2, Fig. 5, 6).

Internal and morphometric indices

There were significant differences in internal (GSI, HSI, gut index) and morphometric indices (eye index) between female and male but only fin index showed no difference between sexes (Table 1). The most of internal and morphometric indices were significantly different between silvering stage S1 and S2 (Table 1). But the some other indices (HSI, fin index of females, eye index of males, gut index of fe-

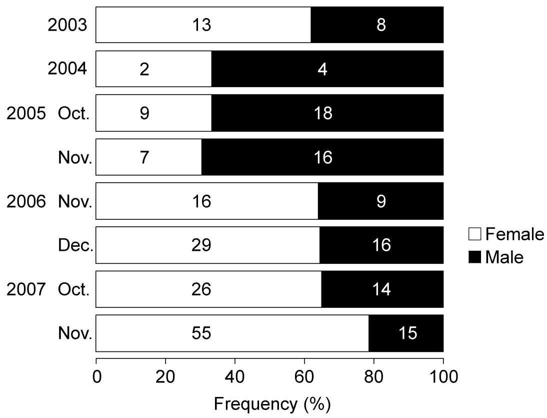

Fig. 2. Frequency composition of female (white) and male (black) of silver-phase Japanese eel collected from Hamana Lake from 2003 to 2007. The number within each bar indicates the number of each sex.

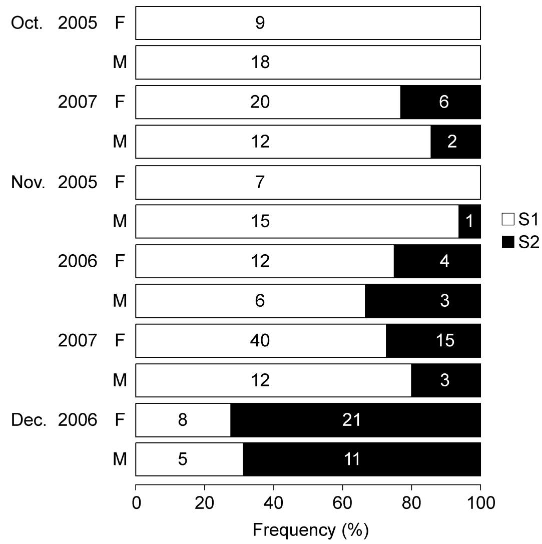

Fig. 3. Frequency composition of silvering stage S1 (white) and S2 (black) of silver-phase Japanese eel collected from Hamana Lake from 2005 to 2007. The number within each bar indicates the number of each stage.

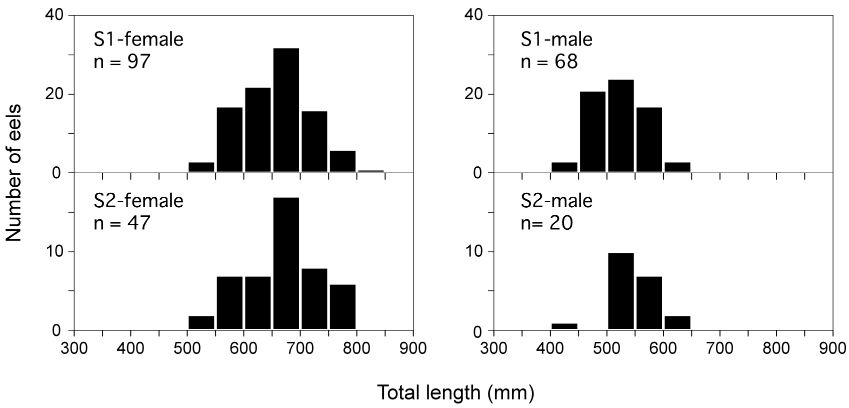

Fig. 4. Length distribution of silver-phase Japanese eels collected from Hamana Lake.

Table 2. General linear model for size and condition of silver-phase Japanese eels in Hamana Lake collected from 2003 to 2007.

	Variable	df	MS	*F*	p
Size	Intercept	1	67835.7	20.07	<**0.001**
	Sex	1	913200.8	270.23	<**0.001**
	Year	4	5517.4	1.63	>0.16
	Month	1	253.4	0.07	>0.78
	Year×Month	4	5973.0	1.77	>0.13
Condition	Intercept	1	0.01	19.28	<**0.001**
	Sex	1	0.00	10.58	<**0.01**
	Year	4	0.00	1.70	>0.15
	Month	1	0.00	1.08	>0.30
	Year×Month	4	0.00	2.05	>0.087

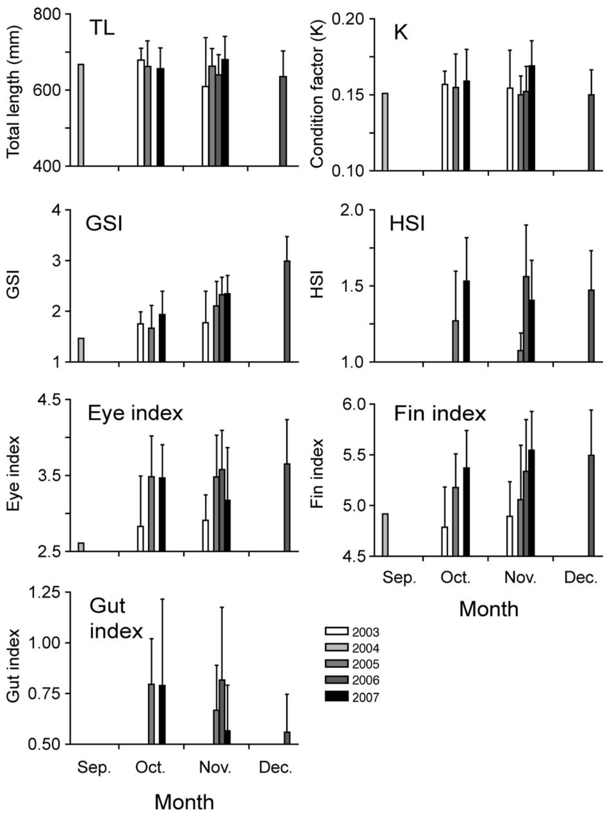

Fig. 5. Monthly mean total length, Fulton's condition factor (K), internal (gonad-somatic index (GSI), hepato-somatic index (HSI), gut index) and morphometric (fin and eye index) indices of female silver-phase Japanese eels in Hamana Lake from 2003 to 2007. Bars indicate standard deviation.

males) were similar between stages. Mean GSI of S2 was higher than S1 in each sex (Mann-Whitney *U*-test, $p<0.001$, Table 1). The mean HSI of the silver females was slightly higher in S1 eels, but this difference was not statistically significant (Mann-Whitney *U*-test, $p=0.07$, Table 1). The mean HSI of the males of S2 was similar to S1 (Mann-Whitney *U*-test, $p=0.21$, Table 1). The mean fin index of the females of S2 was similar to S1 females (Mann-Whitney *U*-test,

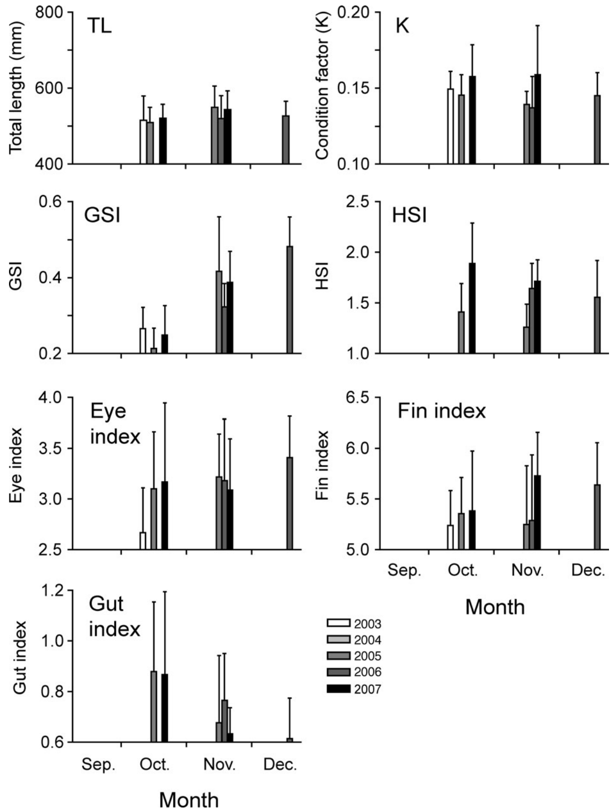

Fig. 6. Monthly mean total length, Fulton's condition factor (K), internal (gonad-somatic index (GSI), hepato-somatic index (HSI), gut index) and morphometric (fin and eye index) indices of male silver-phase Japanese eels in Hamana Lake from 2003 to 2007. Bars indicate standard deviation.

$p=0.10$, Table 1). The mean fin index of the males of S2 was higher than S1 (Mann-Whitney *U*-test, $p<0.01$). The mean eye index of the silver females of S2 was higher than S1 eels (Mann-Whitney *U*-test, $p<0.01$, Table 1). The mean eye index of the S2 males did not differ from S1 (Mann-Whitney *U*-test, $p=0.14$, Table 1). The mean gut index of the silver females of S2 was similar to S1 (Mann-Whitney *U*-test, $p=0.15$, Table 1). The mean gut index of the silver males of S2 was lower than S1 eels (Mann-Whitney *U*-test, $p<0.01$, Table 1).

The relationships among GSI, fin index, eye index, and gut index of both sexes were correlated except HSI (Table 3). All of the correlations among indices without HSI-fin index and gut index-eye index were significant in females ($r^2=0.04$–0.18, $p<0.05$, Table 3). HSI of males had only significant correlation to gut index ($r^2=0.08$, $p<0.01$, Table 3), and other indices of males had significant relationships ($r^2=0.09$–0.29, $p<0.01$, Table 3).

The internal indices changed seasonally but significant change in morphometric indices were not found (Table 4, Fig. 5, 6). GSI, HSI and gut index were different among months revealed by general linear modeling (Month, $p>0.05$–0.001, Table 4). This indicated that there was significant variation in gonad, liver and gut of silver eels among months (Table 4, Fig. 5, 6).

Age and growth

A comparison of the ages and growth rates of the eels whose otoliths were examined showed that there was a wide range of ages and the individual growth rates (Table 5). The age of females (n=78) ranged from 4 to 16 years, with a mean±SD of 9.9±2.6 years, and age of females was higher than those of the males (n=71, mean: 8.3±2.5, range: 3–14 years, Mann-Whitney *U*-test, p<0.001). The mean growth rate of females (n=78, 65.2±20.0 mm/year) was similar to that of males (n=71, 62.2±21.9, Mann-Whitney *U*-test, p=0.12). Female silver eels of stage S1 (n=40, mean: 9.8±1.9 years) were significantly younger than female eels of S2 (n=28, 11.5±1.9 years, Mann-Whitney *U*-test, p<0.001) but those of males were similar between stages (S1: n=48, 8.8±2.1 years; S2: n=12, 9.3±2.5 years, Mann-Whitney *U*-test, p=0.34). The growth rates of female silver eels of stage S1 (n=40, mean: 64.6±15.3 mm/year) were significantly higher than those of S2 (n=28, 54.6±10.6 mm/year, Mann-Whitney *U*-test, p<0.01) but those of males were similar between stages (S1: n=48, 55.6±15.2 mm/year; S2: n=12, 55.8±18.9 mm/year, Mann-Whitney *U*-test, p=0.74).

Sex dependant growth patterns were found in the von Bertalanffy growth curves of silver eels (Fig. 7). The growth coefficients (k) of males had higher value (0.76) than that of females (0.42). Males had rapid growth at first few years of

Table 3. Correlation coefficients among GSI, HSI, fin index, eye index and gut index for males (upper) and female (lower) silver-phase Japanese eels.

	GSI	HSI	Fin index	Eye index	Gut index
GSI	—	<0.01	0.09**	0.18***	0.16***
HSI	0.08***	—	<0.01	0.03	0.08**
Fin index	0.10***	0.01	—	0.29***	0.15***
Eye index	0.09***	0.04*	0.11***	—	0.09**
Gut index	0.18***	0.04*	0.06**	<0.01	—

Significance levels: * p<0.05; ** p<0.01; *** p<0.001.

Table 4. General linear models for internal and morphometric indexes of silver-phase Japanese eels in Hamana Lake collected from 2003 to 2007.

	Variable	df	MS	*F*	p
GSI	Intercept	1	0.31	2.22	>0.14
	Sex	1	190.19	1382.04	<**0.001**
	Year	4	0.40	2.94	<**0.05**
	Month	1	0.87	6.31	<**0.05**
	Year×Month	4	0.44	3.18	<**0.05**
HSI	Intercept	1	3.09	36.55	<0.001
	Sex	1	2.33	27.51	<0.001
	Year	2	0.01	0.13	>0.87
	Month	1	0.65	7.70	<**0.01**
	Year×Month	2	0.03	0.38	>0.68
Fin index	Intercept	1	3.43	17.67	<**0.001**
	Sex	1	0.65	3.35	>0.06
	Year	4	0.24	1.25	>0.29
	Month	1	0.06	0.32	>0.56
	Year×Month	4	0.29	1.47	>0.21
Eye index	Intercept	1	2.53	7.79	<**0.01**
	Sex	1	3.88	11.96	<**0.001**
	Year	4	0.70	2.15	>0.07
	Month	1	0.13	0.41	>0.52
	Year×Month	4	0.77	2.37	>0.05
Gut index	Intercept	1	3.73	53.99	<**0.001**
	Sex	1	0.12	1.73	>0.19
	Year	2	0.01	0.15	>0.86
	Month	1	2.16	31.28	<**0.001**
	Year×Month	2	0.01	0.11	>0.89

Table 5. Age, growth rate and parameters of von Bertaranffy curve of silver-phase Japanese eels collected in Hamana Lake from 2003–2007.

Sex	*n*	Age (year)	Growth rate (mm/year)	L_{∞}	*k*	t_o
Female	78	9.9±2.6 4–16	65.2±20.0 41.2–131.3	677.9	0.42	−0.22
Male	71	8.3±2.5 3–14	62.2±21.9 28.4–123.0	528.1	0.76	−0.16

Note: upper numbers of age and growth rate: mean±SD; lower: range.

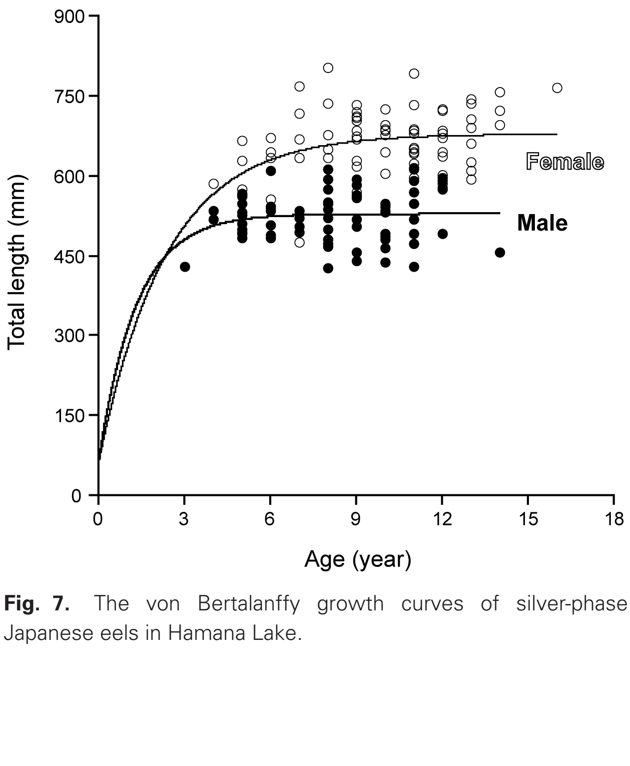

Fig. 7. The von Bertalanffy growth curves of silver-phase Japanese eels in Hamana Lake.

growth phase until 3 years, whereas females attained larger maximum size (L_∞) with 677.9 mm than males (528.1 mm) (Table 5, Fig. 7).

Discussion

Sex ratio

The sex determination of anguillid eels is thought to be caused by environmental factors (Krueger and Oliveira 1999, Davey and Jellyman 2005). It is well known that the sex differentiation was determined not by age but the body size, which means that the fast growing individuals differentiate earlier than the slow growing individuals. Previous research has suggested that the factors that determine the sex of anguillid eels are probably related to environmental factors such as density (DeLeo & Gatto 1996; Holmgren 1996; Krueger & Oliveira 1999), because high densities of eels appear to have caused elevated proportions of males in cultured European and American eels (Roncarati et al. 1997; Krueger & Oliveira 1999).

In this study, the relatively high proportion of males (39%) and larger number of males (n=100) were found comparing to other ecological studies in this species range. Kotake et al. (2007) reported that 5–30% of the Japanese eels were males in Mikawa Bay (n=24) and Amakusa Isrands (n=13). Previous studies conducted in river habitats in Taiwan showed a lower proportion of males (Han et al. 2003a: 12.4%, Tzeng et al. 1995: 7.2%). This difference in the collections suggested that differing environmental conditions among the sites when eels attain the size at sex determination may influence sex determination in this species. Similar variations in sex ratios were reported in American eel, *Anguilla rostrata* by Oliveira and McCleave (2000), who reported that the sex ratios of silver eels were different among four rivers (percent of males: 49–77%). In anguillid eels, it is thought that high density appear to give rise to males and that low densities favors females (Tzeng et al. 1995, Krueger and Oliveira 1999, Davey and Jellyman 2005). This is supported by the presence of only males in some small streams that have strong recruitment and high densities of yellow-phase American eels (Oliveira 1999).

There was significant variation in the sex ratio among years in this study (Fig. 2). The highest proportion of males of this study was found at November 2005 (70%) and the lowest proportion of males was found at November 2007 (21%). Recently, Laffaille et al. (2006) showed a gradual shift in the silver eel sex ratio from a dominance of males to females according to the changes in the numbers of silver-phase European eels in the same river over a 9-year period. Han and Tzeng (2006) proposed that the sex ratio of eels in a catchment could be regarded as an indicator of the local population status such as abundance of the local stock. Inter-annual variation in the sex ratio observed in this study might also indicate the status of the local eel population in the Hamana Lake system. However, long-term quantitative surveys of biomass, density and sex ratio of the eels in each habitat will be required for precise understanding of local population status. In addition, duration of growth-phase (represented by age at silvering) in each location is also required in the further study, because the sex ratio of silver eels could be affected by the age structure of eels in each habitat and the sex-dependant difference in maturation age.

Maturity of silver eels

The knowledge on levels of maturation of Japanese eels as they begin their spawning migration is still limited. In the present study, the mean value of GSI for female silver eels ranged from 0.47 to 4.03 and those of male silver eels ranged from 0.10 to 0.74. Sasai et al. (2001) reported that the GSI values of female silver eels collected in the East China Sea ranged from 1.3 to 3.5 and those of migrating males ranged from 0.2 to 0.6. Kotake et al. (2007) collected silver eels from Mikawa Bay and Amakusa Islands and reported that GSI of females ranged from 1.0 to 4.3 and those of males ranged from 0.0 to 0.5. Therefore, the GSI values of female silver eels in this study were as high as or higher than those collected in offshore or other areas, and were higher than some silver eels collected during their downstream migration in freshwater area in Japan (1.1–2.5, Sasai et al. 2001) or those of yellow eels in the Hamana Lake system (mean 0.35 for females, 0.12 for males, Yokouchi et al. 2008). In the artificial maturation of Japanese eel, the GSI level reaches 30–60 at the final stage of maturation (Satoh et al. 1992, Sato et al. 2003). Thus, all the GSI values observed in wild eels have been much lower in comparison with artificially matured eels, implying that silver eels continue to mature during the long migration to the spawning area in the open ocean.

Downstream migrating female European eels typically have GSI values of >1.2 (Vollestad and Jonsson 1986, Durif et al. 2005) but lower than 3.0 (Svedäng and Wickström 1997, Durif et al. 2005). Comparing the maximum GSI values of females, silver-phase Japanese eels (max=4.03, this study) had higher maximum value than those of silver-phase European eels. Also, The mean gut index of silver-phase Japanese eels (this study: 0.66–0.74, Okamura et al. 2007: 0.5–0.6) are lower than that of European eels (1.18–1.84, Durif et al. 2005). Thus, these results indicated that silver-phase Japanese eels have comparatively higher maximum GSI values, and lower value of gut index comparing to European eels. In contrast, *A. bicolor bicolor* collected from the Re'union Island (Robinet et al. 2003) and *A. dieffenbachii* in a New Zealand estuary (Lokman et al. 1998) were characterized a more advanced sexual maturation status (GSI: 6.78 for *A. bicolor bicolor*, 7.22 for *A. dieffenbachii*) than most *Anguilla* silver eel species at the onset of seaward spawning migration (Lokman et al. 1998, Robinet et al. 2003). These results could suggest that it could corroborate the short scale migration of these two tropical species to the spawning grounds (Robinet et al. 2003). Therefore, it could be suggested that the difference in maturity of the silver eels in the beginnings of their spawning migration between Japanese eels and European eels might be reflect by the difference in their distance to the spawning area (Japanese eel: ca. 3000 km, European eel: ca. 6000 km).

Silvering index

Recently, the specific silvering index was made for the Japanese eel. Okamura et al. (2007) defined four silvering stages in Japanese eel in a coastal area of Japan (Mikawa Bay) using the colorations of various body parts of the eels (Y1, Y2, S1 and S2). S2 eels had significantly higher maturity than that of S1 eels, and the later timing of occurrence than S1 eels in Mikawa Bay (Okamura et al. 2007). This is similar to the results of this study in Hamana Lake. This is further supported by the occurrence of highly matured eels migrating offshore observed by Sasai et al. (2001) having the same appearance with the S2 eels. It was suggested that the S2 eel can be a more advanced stage of typical silver eel with the progress of season but regardless the location.

Correspondingly to four silvering stages of the Japanese eel (Y1–S2, Okamura et al. 2007), Durif et al. (2005) found five silvering stages (stage I–V) in the European eel in France using various parameters such as the TL, condition factor, eye diameter, pectoral fin length, GSI, HSI, gut index. The mean GSI, fin index and gut index values of silver-phase Japanese eels were relatively similar to those of silver-phase European eels. For example, the mean fin index values of silver-phase Japanese eels (5.38–5.39, this study) are similar to those of European eels (4.3, 5.0, respectively in stage IV, V: Durif et al. 2005). On the other hand, mean eye index values of European eels were extremely higher (4.5–10.8, stage I–V: Durif et al. 2005, 2.0–4.8, stage I–III: Yokouchi et al. 2009) than those of Japanese eels (2.5–6.4: Okamura et al. 2007, 3.1–3.6: this study) regardless the stage (yellow or silver). In the Japanese eel, GSI was correlated to the eye index (this study, Han et al. 2003a). Durif et al. (2005) suggested that eye index was not correlated to GSI in silver-phase European eels. For American eels, the eye size was not correlated to gonadal development because of the variability of eye size (Han et al. 2002). Therefore, it is suggested that eye index have a species-specific values and could reflect exactly the gonadal maturity at least for the Japanese eel.

Age and growth

This study found a wide range of ages and growth rates, with the females reaching older ages than the males. The mean age of females (9.9 years) were older than those of the males (8.3 years). Although the mean growth rate of females (65.2 mm/year) were similar to that of males (62.2 mm/year), males had higher growth coefficient (k=0.76) in the von Bertalanffy growth curve than that of females (0.42). This is similar to other location of this species and to other species of anguillid eels in which the females reach much larger sizes and older ages than the males (Tzeng et al. 2000, 2002, Han et al. 2003a, Vøllestad 1992, Pool and Reynolds 1996, Krueger and Oliveira 1997, Walsh et al. 2006). The result of this study indicated that males had faster growth in younger age than females. In fact, the younger sex-undifferentiated eels examined by Yokouchi et al. (2008) had higher overall growth rates in Hamana Lake where males were more dominant than in the adjacent river. These differences could be explained by the difference in life history strategies adopted by males and females similarly to American eels (Helfman et al. 1987). Male eels use ‘a time-minimizing life history strategy’ to migrate at the earliest possible age and minimum size that can mature and swim back to the spawning area, while females use ‘a size-maximizing strategy’ and migrate when a maximum body size for trade-off of fecundity has been achieved (Helfman et al. 1987).

The results of this study suggest that, silver-phase Japanese eels have a wide range of the biological characteristics, but significant differences can occur in sex ratio, the proportion of silvering stages among years and in internal indices within silver-phase during their downstream migration season. The factors that may influence biological characteristics of eels in their silvering are complex and require further study. Thus, it is important to investigate the migratory behavior and ecological strategy of eels inhabiting rivers to the coastal habitats with environmental and biological gradients of factors such as temperature, salinity, density of eels and food availability to gain a better understanding of eel ecology.

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